NORTH AMERICAN STIPEAE (GRAMINEAE): TAXONOMIC CHANGES AND OTHER COMMENTS¹

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ABSTRACT

The generic treatment of North American Stipeae is substantially modified. Seven genera are recognized, Achnatherum, Piptatherum, Oryzopsis, Ptilagrostis, Piptochaetium, Nassella, and Hesperostipa. Only Hesperostipa has not previously been recognized at the generic level. The characteristics of each genus are summarized and the 45 new combinations necessitated by this treatment presented. All species occurring in the continental U.S.A. and Canada are treated, plus a few of those occurring in northern México. The largest genus, both globally and regionally, is Achnatherum. Hesperostipa comprises four species, H. comata, H. spartea, H. curtiseta, and H. neomexicana. The taxonomic changes at the specific level are 1) the description of a new species, A. perplexum, 2) modification of the limits of A. lobatum, A. occidentale, and A. coronatum, and 3) selection of a neotype for Stipa robusta (Vasey) Scribner.

KEY WORDS: Gramineae, Stipeae, Taxonomy, Nomenclature, North America

The Stipeae is a cosmopolitan tribe comprising approximately 500 species. The limits of the tribe are now well accepted. Its members have a single floret per spikelet, with no rachilla extension, glumes that usually extend beyond the lemma apex, a well developed callus, a lemma that is usually stiff or hard, and a terminal, usually articulated awn. Anatomically, the tribe seems to be united by having a 95-130° angle between the coleorhiza and coleoptile (Reeder

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1957; Matthei 1965; Barkworth 1982), but this character has been examined in relatively few species.

The generic interpretation of the Stipeae in most North American floras is based on A.S. Hitchcock's (1935, 1951) treatments which recognize three genera in North America, Stipa, Oryzopsis, and Piptochaetium. Some modifications of these genera have been proposed (e.g., Parodi 1944; Johnson 1945a; Spellenberg & Mehlenbacher 1971) but the widespread adoption of Hitchcock's generic treatment has limited their adoption. This paper presents the combinations used to treat the North American Stipeae in the forthcoming Jepson Manual and Manual of North American Grasses. I have included a key to the genera and generic descriptions, and listed the species within each genus that occur in the continental U.S.A. and Canada. Where changes in species delimitation are proposed, the reasons for the change are summarized following the appropriate name.

The discrepancy between traditional treatments of the Stipeae and the phylogenetic history of the tribe was first convincingly demonstrated by Parodi (1944). He showed that species sharing a number of highly unusual leaf and floret characteristics were being placed in two different genera, Stipa and Piptochaetium, because traditional treatments emphasized ecologically adaptive features of the floret, callus, and awn. As a result of his studies, Parodi (1944) transferred several species from Stipa to Piptochaetium, including two species that occur in the U.S.A., P. avenaceum and P. pringlei.

Thomasson (1976, 1978, 1979) provided additional evidence supporting Parodi's expansion of Piptochaetium and recommended the expansion of Nassella to include several species then included in Stipa, but made no formal nomenclatural proposals. Thomasson also stated that, even with the nasselloid species of Stipa excluded, Stipa as interpreted in North America included representatives of two different lineages. My studies (Barkworth 1981, 1982, 1983, 1990; Barkworth & Everett 1987) corroborated and extended Thomasson's conclusions. Barkworth (1990) revised the limits of Nassella and outlined the "major groups" of American Stipeae. In this paper, I formalize the treatment of these groups for the U.S.A. and Canada, and include the names of one Mexican species examined by Hoge (1992). For each new combination or name, only the basionym and the synonyms in current use are shown. A more complete listing of synonymy can be found in A.S. Hitchcock (1951). Making the changes needed for the 150-200 American species occurring south of the Mexican-U.S.A. border was beyond the scope of this study. I encourage others to pursue the task.

KEY TO THE GENERA OF NORTH AMERICAN STIPEAE

1. Palea longitudinally grooved and longer than the lemma, protruding from

- Palea flat, shorter than or equaling the lemma, usually not protruding at the lemma apex (awnlike tips of the veins protruding in A. stillmanii); lemma margins flat.
 - Lemma margins strongly overlapping; palea less than one third the length of the lemma, glabrous and ecostate. Nassella
 - Lemma margins not or only slightly overlapping; palea from one third the length of the lemma to equaling it, usually pubescent (always pubescent if short), 2 veined.
 - Palea usually pubescent and shorter than or equal to the lemma, its apex flat; palea veins usually terminating below the apex; lemma usually coriaceous but not indurate.
 - Palea often glabrous, always as long as the lemma, its apex appearing prow tipped or "pinched"; veins terminating at the apex; lemma indurate.
 - 5. Florets more than 7.5 mm long; callus sharp. Hesperostipa
 - 5. Florets less than 7.5 mm long; callus blunt.
 - 6. Florets dorsally compressed; lemma margins not overlapping, the palea exposed, at least in part. Piptatherum
 - 6. Florets terete or laterally compressed; lemma margins often overlapping, concealing the palea. Oryzopsis

NOTE: New names or combinations are presented in bold face; existing names are italicized and presented only to clarify the limits of each genus in North America.

ACHNATHERUM P. Beauvois

Plants tufted, sometimes with short rhizomes. Culms erect, not branching. Ligules membranous, sometimes ciliate, the hairs sometimes exceeding the membranous portion; collar sometimes ciliate; blades conduplicate, involute, or convolute. Panicle usually contracted, varying to open. Glumes

longer than the floret, usually tapering from midlength or below, with 1, 3 or 5 evident veins, the apex acute to acuminate; floret terete, usually ellipsoidal to cylindrical, sometimes globose; callus 0.2-2 mm long, blunt or sharp, usually strigose above; lemma stiffly membranous to coriaceous, rarely indurate, usually pubescent, the hairs usually evenly distributed, sometimes conspicuous; lemma apex generally with membranous lobes 0.5-2 mm long, these occasionally thick or awnlike; awn 3-80 mm, usually scabrous to scabridulous, sometimes pilose in whole or in part, if more than 1 cm long, persistent, twisted below and once or twice geniculate, if less than 1 cm, readily deciduous, scarcely twisted and nongeniculate; palea from 1/3 the length of the lemma to equaling it, pubescent (ours) or glabrous, similar in texture to the lemma, 2 veined, the veins usually terminating before the rounded apex (veins extended in A. stillmanii). LECTOTYPE (Niles & Chase 1925): Achnatherum calamagrostis (L.) P. Beauvois. Name from the Greek, achne, scale, and ather, awn, a reference to the awned lemma.

A.S. Hitchcock (1925, 1935, 1951) included the short awned species of Achnatherum in Oryzopsis and the long awned species in Stipa. The treatment of Achnatherum adopted here is broader than that adopted by Tzvelev (1976) and Tutin (1980) but consistent with the interpretation of Keng (cited in Tzvelev 1977), Tzvelev (1977), and Lu & Kuo (1987). It is also supported by lemma epidermal pattern (Thomasson 1976, 1978, 1979; Barkworth & Everett 1987) and epiblast morphology (Matthei 1965; Barkworth 1982, 1990), to the extent that these characteristics have been investigated. The association of short, rounded florets with short, deciduous awns, characters that would place a species in Oryzopsis sensu Hitchcock (1935, 1951; Johnson 1945a), is a consequence of selection for endozochoric dispersal (Parodi 1944) by consumption.

Under the interpretation presented here, Achnatherum becomes the largest and most widespread genus in the Stipeae. It occurs in Australia, Eurasia, Africa, New Zealand, and South America as well as North America, although it has not yet been recognized nomenclaturally in Australasian, African, and South American floras. In the Americas and Eurasia, its members appear to be associated with montane regions. It is unclear whether the North American species are descended from South American or Eurasian ancestors, or both. I consider that Achnatherum is more closely related to Piptatherum, Ptilagrostis, and Stipa sensu stricto (Barkworth 1990) but Thomasson (1976, 1979, 1989 in litt.) argued that its closest relative is Nassella.

Most North American species of Achnatherum are, morphologically, rather uniform and resemble species found in Eurasia and other parts of the Americas. A few species, formerly included in Oryzopsis, are distinctive in having shorter florets and readily deciduous, short awns. There is at least one distinctive subgroup among the South American taxa that is not represented in the U.S.A. or Canada. Members of this subgroup have strongly tapering

florets, a glabrous, stiff palea and a lemma with long, divergent apical hairs. One representative, A. papposum, has been collected in California. Formal recognition of such infrageneric groups would, however, be premature without a comprehensive study of the genus.

Achnatherum stillmanii is anomalous among North American species of Achnatherum because it is rhizomatous, averages over 1.5 m in height, has awnlike lobes at the lemma apex, paleas with veins that extend as awnlike tips above the top of the lemma, and because of its lemma epidermal pattern. It appears to be more closely related to sect. Aristella (Trinius) Tzvelev [= Stipa sect. Achnatheropsis Tzvelev], which includes A. bromoides (L.) P. Beauvois, than to sect. Protostipa Tzvelev, to which most of our species belong.

The most difficult aspect in circumscribing Achnatherum is determining how to treat the Australian taxa, all of which are now included in Stipa. If included in Achnatherum, the range of variation within the genus would have to be expanded to include, for instance, branched culms and a sulcate palea, but it would still be a smaller and more uniform genus than Stipa sensu Hitchcock (1951).

Acceptance of Achnatherum is not universal. Clayton & Renvoize (1986) included it in Stipa without comment. Freitag (1985) adopted a broader concept of Stipa than Clayton & Renvoize (1986), based on species that he considered morphologically intermediate between Achnatherum, Stipa, Trikeraia, and Ptilagrostis. These taxa are part of the same evolutionary line within the tribe, but micromorphological, anatomical, and cytological data suggest that Stipa should either be expanded to include several North American species currently placed in Oryzopsis, an option not discussed by Freitag (1985) or Clayton & Renvoize (1986), or split into a number of more uniform segregate genera, the alternative I prefer.

Achnatherum altum (Swallen) Hoge & Barkworth, comb. nov. BASIONYM:

Stipa alta Swallen; Proc. Biol. Soc. Wash. 56:79 (1943). TYPE: US

2209361!; MEXICO. Coahuila: Sierra de la Madera, Municipio Cienegas,
Cañon del Aqua; 10 September 1939; C.H. Muller 3261.

Achnatherum altum is sometimes included in A. lobatum, but has longer ligules (0.9-5.2 mm vs. 0.3-0.9 mm) and shorter lemma lobes (0.2-0.7 mm vs. [0.4]0.6-1.2 mm). Marshall Johnston, in his Flora of the Chihuahuan Desert (unpubl.) comments that plants referable to A. altum [as Stipa alta] intergrade with typical members of A. lobatum. Hoge (1992) examined specimens referable to these and five other taxa during her study of A. perplexum. Although there was overlap in individual characters, the two taxa are distinct, based on an assessment of overall morphological similarity using Gower's distance measure and enzyme similarities (Hoge 1992). Achnatherum altum is restricted to México.

- Achnatherum aridum (M.E. Jones) Barkworth, comb. nov. BASIONYM: Stipa arida M.E. Jones, Proc. Calif. Acad. Sci., Ser. 2, 5:725 (1895). TYPE: UNITED STATES. Utah: Marysvale; M.E. Jones 5977.
- Achnatherum brachychaetum (Godron) Barkworth, comb. nov. BA-SIONYM: Stipa brachychaeta Godron, Mém. Sect. Sci. Acad. Sci. Montpellier 1:450 (1853).

This species, which is listed by the federal government in the U.S.A. as a noxious weed, was collected on ballast near Portland, Oregon, and occurs in portions of California. It is native to Uruguay and central Argentina. Barkworth (1990) mistakenly transferred it to Nassella. I apologize for any consequent confusion and thank those who brought it to my attention.

- Achnatherum clandestinum (Hackel) Barkworth, comb. nov. BASIONYM:

 Stipa clandestina Hackel, Repert. Spec. Nov. Regni Veg. 8:516 (1910).

 LECTOTYPE: MEXICO. prope Michoacán; Arsène 3441 [designated by A.S. Hitchcock (1925)].
- A.S. Hitchcock (1925) describes this species as occurring from northern México to Colombia. It is now established in Texas (Barkworth et al. 1989). Collections have also been made in San Luis Obispo, California (Curto 611, UTC 206571) but Curto stated later (in litt.) that it had since been eliminated from the garden where he found it. Because Achnatherum clandestinum has the potential for being a significant problem in rangelands, its spread should be strongly discouraged.
 - Achnatherum contractum (B.L. Johnson) Barkworth, comb. nov. BA-SIONYM: Oryzopsis hymenoides (Roemer & Schultes) Ricker var. contracta B.L. Johnson, Bot. Gaz. 107:24 (1945).

This species, which is known only from the Big Hollow area of southeastern Wyoming, is the fertile derivative of an Achnatherum hymenoides -Piptatherum micranthum (Trinius & Ruprecht) Barkworth hybrid (Shechter 1965; Shechter & Johnson 1966, 1968). I place it in Achnatherum because it is more similar to that genus than it is to Piptatherum.

- Achnatherum coronatum (Thurber) Barkworth, comb. nov. BASIONYM:
 Stipa coronata Thurber in S. Watson, Bot. California 2:287 (1880). SYNTYPES: UNITED STATES. California: Julian; Bolander, and San
 Bernardino, Parry & Lemmon 422.
- A.S. Hitchcock (1951) and others interpreted this species to include Achnatherum parishii, but it is generally larger than that species, has twice geniculate

awns, and paleas with shorter, less dense pubescence than A. parishii. It also tends to have somewhat longer trichomes at the top of its leaf sheath (1.25-4.40 mm, averaging 2.6 mm; rather than 0.7-4 mm, averaging 1.9 mm in A. parishii subsp. parishii). The range of A. coronatum extends from the San Francisco Bay area south through the coastal mountains to Baja California.

Achnatherum curvifolium (Swallen) Barkworth, comb. nov. BASIONYM:
Stipa curvifolia Swallen, J. Wash. Acad. Sci. 23:456 (1933). HOLOTYPE: US 1538063!; UNITED STATES. New Mexico: Eddy County,
Guadalupe Mountains; Wilkins 1660.

In the U.S.A., this species is known only from the Guadalupe Mountains of Texas and New Mexico and from Dona Ana County, New Mexico, but it also occurs in northern México.

Achnatherum diegoense (Swallen) Barkworth, comb. nov. BASIONYM: Stipa diegoensis Swallen, J. Wash. Acad. Sci. 30:212, f. 2 (1940). HOLOTYPE: US 1761177!; UNITED STATES. California: San Diego County; Gander 5778.

This species extends from San Diego County north to the Channel Islands of California (Ferren et al. 1986). It differs from other species of Achnatherum primarily in having distinctly pubescent nodes.

- Achnatherum eminens (Cavanilles) Barkworth, comb. nov. BASIONYM: Stipa eminens Cavanilles, Icon. 5:42, pl. 46, f. 1 (1799). TYPE: MEX-ICO. Chalma.
- Achnatherum hendersonii (Vasey) Barkworth, comb. nov. BASIONYM:
 Oryzopsis hendersonii Vasey, Contr. U.S. Natl. Herb. 1(8):267 (1893).
 TYPE: UNITED STATES. Washington: North Yakima, Clements
 Mountain; Henderson 2249.

Mehlenbacher (1970; Spellenberg & Mehlenbacher 1971) transferred this species to Stipa after demonstrating that it was closely related to Stipa lemmonii (Vasey) Scribner [=Achnatherum lemmonii (Vasey) Barkworth]. It is unusual in Achnatherum in having a shiny, indurate, glabrous floret. The indurate nature of the lemma reflects the relatively large number of layers between the two epidermal layers. The pattern of the outer epidermal layer is similar to that in most other species of Achnatherum (Thomasson 1976, 1978, 1979 [his "robusta" type]; Barkworth & Everett 1987).

Achnatherum hymenoides (Roemer & Schultes) Barkworth, comb. nov. BASIONYM: Stipa hymenoides Roemer & Schultes, Syst. Veg. 2:339 (1817). TYPE: UNITED STATES. banks of the Missouri River; Bradbury. Achnatherum hymenoides has frequently been cited in discussions of generic limits within the Stipeae (Johnson & Rogler 1943; Johnson 1945a, 1945b, 1962, 1972; C.L. Hitchcock & Spellenberg 1968; Kam & Maze 1974; Barkworth & Everett 1987). Although it was usually placed in Oryzopsis because of its ovoid caryopsis and short, readily deciduous awn, it hybridizes with many of the species of Stipa that are here transferred to Achnatherum. It also, however, hybridizes with Piptatherum micranthum [= Oryzopsis micrantha (Trinius & Ruprecht) Thurber] (Shechter 1965; Shechter & Johnson 1966, 1968; see Achnatherum contractum), Nassella viridula (Trinius) Barkworth (Johnson & Rogler 1943; see × Achnella caduca [Beal] Barkworth below), and Hesperostipa neomezicana (Weber 1957). Except in the case of A. contractum, the hybrids are completely sterile. Morphological and anatomical evidence support its inclusion in Achnatherum (Kam & Maze 1974; Barkworth & Everett 1987).

Achnatherum latiglume (Swallen) Barkworth, comb. nov. BASIONYM:
Stipa latiglumis Swallen, J. Wash. Acad. Sci. 23:198, f. 1 (1933). HOLOTYPE: US 992334!; UNITED STATES. California: Yosemite Valley,
Camp Lost Arrow; 22 June 1911; Abrams 4469.

Pohl (1954) demonstrated that Achnatherum latiglume is an alloploid derivative of Stipa elmeri Piper & Brodie ex Scribner [=A. occidentale (Thurber) Barkworth subsp. pubescens] and S. lemmonii [= A. lemmonii].

Achnatherum lemmonii (Vasey) Barkworth, comb. nov. BASIONYM:
Stipa pringlei Scribner var. lemmonii Vasey, Contr. U.S. Natl. Herb.
3(1):55 (1892). TYPE: UNITED STATES. California: Plumas County;
J.G. Lemmon 5456. Stipa lemmonii (Vasey) Scribner, U.S.D.A. Div.
Agrostol. Circ. 30:3 (1901).

Stipa lemmonii (Vasey) Scribner var. jonesii Scribner, U.S.D.A. Div. Agrostol. Circ. 30:4 (1901). TYPE: UNITED STATES. California: Emigrant Gap; M.E. Jones 3298.

Achnatherum lemmonii (Vasey) Barkworth subsp. pubescens (Crampton) Barkworth, comb. et stat. nov. BASIONYM: Stipa lemmonii (Vasey) Scribner subsp. pubescens Crampton, Leafl. W. Bot. 7:220 (1955). HOLOTYPE: DAV!; UNITED STATES. California: Tehama County, Whitlock Camp-Round Mountain area west of Paskenta, serpentine slopes in chaparral, elevation about 4000 ft; 16 June 1954; Crampton 2000.

Crampton cited two specimens in his description of the species, the type collection and Suksdorf 8661. Dibble & Griggs (1979) observed plants in three populations in Tehama and Lake counties, California. They noted that the most pubescent plants were on decomposed serpentine soils, those with intermediate pubescence were on undecomposed serpentine, and glabrous plants

were on nonserpentine soils. Barkworth & Linman (1984) argued against recognition of Stipa lemmonii var. pubescens because specimens with varying degrees of pubescence occurred throughout the range of the species, on both serpentine and non-serpentine soils. The specimens they examined included two duplicates of Suksdorf 8661 but not Crampton 2000, the type of var. pubescens. In 1987, I borrowed the type and other specimens of var. pubescens from DAV and discovered that, unlike the other pubescent specimens (including Suksdorf 8661), they were densely tomentose rather than villous. I therefore decided to recognize Crampton's taxon but consider it to be restricted to Tehama and Lake counties of California.

- Achnatherum lettermanii (Vasey) Barkworth, comb. nov. BASIONYM:
 Stipa lettermanii Vasey, Bull. Torrey Bot. Club 13:53 (1886). TYPE:
 US556904!; UNITED STATES. Idaho: Snake River; G.W. Letterman
 102.
- Achnatherum lobatum (Swallen) Barkworth, comb. nov. BASIONYM: Stipa lobata Swallen, J. Wash. Acad. Sci. 23:199, f. 2 (1933). HOLO-TYPE: US905722!; UNITED STATES. New Mexico: Guadalupe Mountains, Queen Ranger Station; A.S. Hitchcock 13502.
- Achnatherum nelsonii (Scribner) Barkworth, comb. nov. BASIONYM:

 Stipa nelsonii Scribner, U.S.D.A. Div. Agrostol. Bull. 11:46 (1898).

 TYPE: US 556901!; UNITED STATES. Wyoming: Albany; A. Nelson 3963.
- Achnatherum nelsonii (Scribner) Barkworth subsp. dorei (Barkworth & Maze) Barkworth, comb. nov. BASIONYM: Stipa nelsonii Scribner subsp. dorei Barkworth & Maze, Taxon 28:623 (1979). TYPE: DAO!; CANADA. Alberta: Dungarvan Creek; W.G. Dore 12136.
- Achnatherum nelsonii (Scribner) Barkworth subsp. longiaristatum (Barkworth & Maze) Barkworth, comb. et stat. nov. BASIONYM: Stipa nelsonii Scribner var. longiaristata Barkworth & Maze, Taxon 28:623 (1979). TYPE: WS!; UNITED STATES. Washington: 8-9 mi west of Spokane; J.S. Swallen 6231.

This taxon is a puzzling entity. If the hairs on its awns were longer, it would fit easily within Achnatherum californicum. I have elevated it to a subspecies because it is as morphologically and geographically distinct from subsp. nelsonii as is subsp. dorei.

Achnatherum nevadense (B.L. Johnson) Barkworth, comb. nov. BA-SIONYM: Stipa nevadensis B.L. Johnson, Amer. J. Bot. 49:257 (1962). TYPE: UC; UNITED STATES. California: Mono County, Upper Twin Lake, near Bridgeport; B.L. Johnson 211. Johnson (1962) demonstrated that this species is an alloploid derivative of Achnatherum lettermanii and A. occidentale.

Achnatherum occidentale (Thurber) Barkworth, comb. nov. BASIONYM:

Stipa occidentalis Thurber in S. Watson in King, Geol. Expl. 40th Parallel 5:380 (1871). TYPE: GH!; UNITED STATES. California: Yosemite Trail; Bolander 5038.

Achnatherum occidentale (Thurber) Barkworth subsp. pubescens (Vasey)
Barkworth, comb. nov. BASIONYM: Stipa viridula Trinius var. pubescens
Vasey, Contr. U.S. Natl. Herb. 3(1):50 (1892). TYPE: UNITED STATES.
Washington: Columbia River; Suksdorf s.n. [Isotype: US 79560!]. Stipa
occidentalis Thurber var. pubescens (Vasey) Maze, Taylor, & MacBryde,
Canad. J. Bot. 56:193 (1978).

Stipa elmeri Piper & Brodie ex Scribner, U.S.D.A. Div. Agrostol. Bull. 11:46 (1898).

This species is interpreted as comprising only plants with pilose awns, i.e., A.S. Hitchcock's (1951) Stipa occidentalis, S. elmeri, and S. californica Merrill & Burtt Davy but not S. nelsonii, S. williamsii Scribner, or S. columbiana Macoun. Specimens from lower elevations (generally below 3000 m) are pilose only on the first two awn segments whereas those from higher elevations are often pilose on at least the lower portion of the third segment, with some specimens, including the holotype, being pilose throughout. Higher elevation plants also tend to be shorter and have narrower leaf blades with denser adaxial pubescence than do plants from lower elevations. The name Achnatherum occidentale subsp. pubescens refers to the relatively large, lower elevation plants (Maze 1965; Taylor & MacBryde 1978).

Achnatherum occidentale (Thurber) Barkworth subsp. californicum (Merrill & Burtt Davy) Barkworth, comb. nov. BASIONYM: Stipa californica Merrill & Burtt Davy, Univ. Calif. Pub. Bot. 1:61 (1902). TYPE: UNITED STATES. California: San Jacinto Mountains; Hall 2556.

Maze (1962, 1965), whose recommendations were adopted by C.L. Hitchcock (1969), expanded Achnatherum occidentale (as Stipa occidentalis) to include S. californica, S. nelsonii, and S. columbiana. I concur with Maze with respect to S. californica, as is indicated by the above combination, but prefer to use subspecific rather than varietal rank for major infraspecific taxa with a tendency to occupy different geographic areas. I regard the scabrous awned taxa as specifically distinct (see A. nelsonii) although there are intermediates between A. occidentale and A. nelsonii.

Achnatherum papposum (Nees) Barkworth, comb. nov. BASIONYM:
Stipa papposa Nees in C. Martius, Fl. Bras. Enum. Pl. 2:377 (1829).
TYPE: B; Isotype: US 993503 [Hitchcock (1925); [URUGUAY]. ad Monte-Video; Sellow.

This South American species was collected in Berkeley, California, in 1983. So far as I am aware, it has not become established. It differs from all other North American species in the U.S. and Canada in bearing divergent, long hairs at the top of the lemma.

Achnatherum parishii (Vasey) Barkworth, comb. nov. BASIONYM: Stipa parishii Vasey, Bot. Gaz. 7:33 (1882). TYPE: UNITED STATES. California: San Bernardino Mountains; Parish 1079.

This species differs from Achnatherum coronatum in having once geniculate awns and more densely pubescent paleas. It extends from the San Bernardino Mountains east to Nevada and Arizona.

Achnatherum parishii (Vasey) Barkworth subsp. depauperatum (M.E. Jones) Barkworth, comb. et stat. nov. BASIONYM: Stipa parishii Vasey var. depauperata M.E. Jones, Contr. W. Bot. 14:11 (1912). TYPE: UNITED STATES. Utah: Detroit [a now vanished mining town]; M.E. Jones.

Subsp. depauperatum, as its name suggests, consists of smaller plants than subsp. parishii. It also either lacks or has very short (0.1-0.5 mm) trichomes at the top of its leaf sheaths. It occurs in central, southern, and eastern Nevada and western Utah. A.S. Hitchcock (1925, 1935, 1951) did not distinguish it from subsp. parishii.

Achnatherum perplexum Hoge & Barkworth, spec. nov. HOLOTYPUS: US!; UNITED STATES. New Mexico: Bernalillo County, 1.5 mi east on USFS road 413, 9 mi south of Tijeres on NM 14; 8 September 1985; M.E. Barkworth 4764.

Ab A. lobatum (Swallen) Barkworth brevioribus lobis lemmatium et generaliter angustioribus laminis foliorum; ab A. nelsonii (Scribner) Barkworth subsp. dorei (Barkworth & Maze) Barkworth ciliatis ligulis divergentibus acuminatis glumis recedit.

Plants perennial, cespitose, branching intravaginally. Culms 30-70 cm, mostly glabrous, sometimes scabrous or puberulent below the nodes. Sheaths usually longer than the internodes, glabrous to scabrous, the margins sometimes ciliate; ligules 0.3-0.8 mm long, ciliate; blades 1-3 mm wide, scabrous.

Panicle 6-20 cm long, 1-2 cm wide; branches ascending, often with one very shortly pedicellate or even sessile spikelet. Glumes unequal, scabrous, 3 to obscurely 5 veined, the midvein extending to the apex; lower glume 9-14 mm long, 1.5-2.5 mm wide; second glume 7.5-10.5 mm long, 1.0-1.6 mm wide; callus 0.50-0.85 mm long, blunt; lemma 4.5-6.5 mm long, evenly pubescent, the midbody hairs 0.45-1.0 mm long, the apical hairs 0.9-1.8 mm long; lemma lobes 0.15-0.45 mm long; palea 2.5-3.75 mm long; awn 10.4-19.0 mm long, usually once geniculate; anthers 2.25-4.20 mm long.

One of the most distinctive features of this species is that it flowers in late summer, with fruit maturation occurring in September, whereas our other species of Achnatherum flower in late spring to early summer. Electrophoretic data also support recognition of A. perplexum as a distinct taxon (Hoge 1992). Existing specimens tend to have been identified as A. nelsonii subsp. dorei if they were collected in the northern portion of its range and as A. lobatum if they were collected in the southern portion of its range. So far as is known, A. perplexum is restricted to the southwestern U.S.A.

Achnatherum pinetorum (M.E. Jones) Barkworth, comb. nov. BASIO-NYM: Stipa pinetorum M.E. Jones, Proc. Calif. Acad. Sci., Ser. 2 5:724 (1895). NEOTYPE, designated here: US 236788!: UNITED STATES. Utah: Panguitch Lake; M.E. Jones 6023.

The neotype is an isotype of the holotype that was deposited in RSA but has since been lost (pers. comm., S. Boyd).

Achnatherum richardsonii (Link) Barkworth, comb. nov. BASIONYM: Stipa richardsonii Link, Hort. Berol. 2:245 (1833). TYPE: Grown at Berlin from seed sent by Richardson.

There is now no specimen corresponding to the type of Achnatherum richardsonii in B. A neotype needs to be designated by someone able to search the appropriate herbaria. The species is sufficiently distinctive that lack of a type specimen has not presented a problem.

Achnatherum robustum (Vasey) Barkworth, comb. nov. BASIONYM:
Stipa viridula Trinius var. robusta Vasey, Contr. U.S. Natl. Herb. 1(3):56
(1890). PROPOSED CONSERVED TYPE: US 993051!; UNITED
STATES. New Mexico: G.R. Vasey s.n.

The type of Stipa viridula var. robusta designated by Vasey belongs to Achnatherum lobatum. The two taxa are quite distinct, the most reliable identifying features being the pubescent collar of A. robustum and the short, glabrous palea of Nassella viridula [= Stipa viridula]. These are present on all

specimens, the collar pubescence of A. robustum being particularly well developed on the uppermost leaf. Achnatherum lobatum and the type of S. viridula var. robusta selected by Vasey lack this pubescence but have the long lemma lobes that are characteristic of A. lobatum. The two species are superficially similar, but the robusta epithet has consistently been applied to the tall, stout species with a large, dense panicle that is found from Wyoming to northern México, but not in Trans Pecos, Texas. The name S. lobata has consistently been applied to a southern taxon with long lemma lobes.

The type specimen cited above fits the interpretation of Stipa robusta (Vasey) Scribner found in all existing floras (e.g., Hitchcock 1951; Gould 1975). The principle of priority would require that the name S. robusta be applied to S. lobata and a new name be found for the species currently called S. robusta because the combination S. robusta was published (Scribner 1897) before S. lobata (Swallen 1933). Fortunately, the current edition of the International Code of Botanical Nomenclature (Greuter et al. 1988) permits designation of a different specimen as the type of a species if it can be shown that it would lead to greater nomenclatural stability without creating confusion. I have submitted a paper (Barkworth, submitted) to the Nomenclatural Committee of the International Committee of Plant Taxonomists in which I propose that this option be exercised in order to conserve the application of both S. robusta and S. lobata. Until the Committee reaches a decision, the Code requires that the two names continue to be used in their customary sense.

Achnatherum scribneri (Vasey) Barkworth, comb. nov. BASIONYM: Stipa scribneri Vasey, Bull. Torrey Bot. Club 11:125 (1884). TYPE: US 556905!; UNITED STATES. New Mexico: Santa Fe; Vasey s.n.

Because I confused this species with Achnatherum parishii, Peterson & Annable (1986) reported that it was present in California. Both species have longer hairs at the lemma apex than below and are ciliate at the top of the leaf sheath, but A. scribneri has an elongate, sharp callus and A. parishii has a blunt callus.

Achnatherum speciosum (Trinius & Ruprecht) Barkworth, comb. nov. BASIONYM: Stipa speciosa Trinius & Ruprecht, Mém. Acad. Imp. Sci. Saint-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 5(1):45 (1842). TYPE: LE!; CHILE. Cuming.

Achnatherum splendens (Trinius) Nevski

A.S. Hitchcock (1951) reported that this species was sometimes cultivated in the U.S.A. I have not seen any specimens to document his report. In China, it is planted to protect the edges of irrigation ditches and to control erosion (Lu & Kuo 1987).

Achnatherum stillmanii (Bolander) Barkworth, comb. nov. BASIONYM:
Stipa stillmanii Bolander, Proc. Calif. Acad. Sci. 4:169 (1872). TYPE:
UNITED STATES. California: Sierra Nevada, Blue Canyon; 1870;
Bolander.

Achnatherum stillmanii, a Californian endemic, differs from the other North American species of Achnatherum in its shortly rhizomatous, but tufted, growth form, greater height, awnlike lemma lobes, extruded paleal veins, and lemma epidermal pattern. Morphological and anatomical data suggest that its nearest relatives are in northern India and Tibet.

Achnatherum swallenii (C.L. Hitchcock & Spellenberg) Barkworth, comb. nov. BASIONYM: Oryzopsis swallenii C.L. Hitchcock & Spellenberg, Brittonia 20:164 (1968). HOLOTYPE: WTU 227273; UNITED STATES. Idaho: Clark County, just north of Birch Creek, along Highway 28, near the Lemhi County line; C.L. Hitchcock 23868.

In describing this species, C.L. Hitchcock & Spellenberg (1968, p. 164-5) stated that it had "...the floral features traditionally associated with Oryzopsis ...[but] is, in some respects, both morphologically and cytologically at least as similar to species usually referred to Stipa" and suggested that a revision of the generic boundaries might be appropriate.

- Achnatherum thurberianum (Piper) Barkworth, comb. nov. BASIONYM:
 Stipa thurberiana Piper, U.S.D.A. Div. Agrostol. Circ. 27:10 (1900).
 TYPE: UNITED STATES. Washington: north branch of the Columbia and Okanagan; Pickering & Brackenridge.
- Achnatherum webberi (Thurber) Barkworth, comb. nov. BASIONYM: Eriocoma webberi Thurber in S. Watson, Bot. Calif. 2:283 (1880). TYPE: UNITED STATES. California: Sierra Valley; Bolander. Oryzopsis webberi (Thurber) Bentham ez Vasey, Grasses U.S. 23 (1883). Stipa webberi (Thurber) B.L. Johnson, Bot. Gaz. 107:25 (1945).
- Achnatherum × bloomeri (Bolander) Barkworth, comb. nov. BASIONYM:

 Stipa bloomeri Bolander, Proc. Calif. Acad. Sci. 4:168 (1872). TYPE:

 UNITED STATES. California: Bloody Canyon, near Mono Lake. Oryzopsis bloomeri (Bolander) Ricker, Contr. U.S. Natl. Herb. 11:109 (1906).

 × Stiporyzopsis bloomeri (Bolander) B.L. Johnson, Amer. J. Bot. 32:602 (1945).

As noted above, Achnatherum hymenoides forms sterile hybrids with numerous species of Achnatherum. The hybrids are easily identified by their long and abundant lemma hairs and the intermediate shape of their glumes

and florets. Johnson (1945b) provided a key for identifying the second parent. According to the International Code of Botanical Nomenclature (Greuter et al. 1988), the name A. ×bloomeri applies only to hybrids between A. hymenoides and Stipa occidentalis. I see no value in proposing individual binomials for the other hybrids.

×ACHNELLA Barkworth, hybr. gen. nov. = ACHNATHERUM P. Beauvois × NASSELLA Desvaux

×Achnella Barkworth, hybr. gen. nov.
= Achnatherum P. Beauvois × Nassella Desvaux

×Achnella caduca (Beal) Barkworth, comb. nov. BASIONYM: Oryzopsis caduca Beal, Bot. Gaz. 15:111 (1890). TYPE: UNITED STATES. Montana: Belt Mountains; Scribner.

Johnson & Rogler (1943) showed that × Achnella caduca refers to sterile hybrids between Nassella viridula and Achnatherum hymenoides. Hitchcock (1951) included them in Achnatherum × bloomeri. × Achnella caduca differs from this and other intrageneric hybrids involving A. hymenoides in having sparsely pubescent sheath throats, stiffer lemmas with seven, rather than five, veins and anthers of two different lengths. Each of these characteristics is found in N. viridula.

HESPEROSTIPA (Elias) Barkworth, stat. nov.

Hesperostipa (Elias) Barkworth, stat. nov. BASIONYM: Stipa sect. Hesperostipa Elias, Special Pap. Geol. Soc. Amer. 41:67 (1942). TYPE: Hesperostipa comata (Trinius & Ruprecht) Barkworth [= Stipa comata Trinius & Ruprecht].

Plants densely cespitose. Ligules membranous. Panicles usually contracted. Glumes exceeding the floret, lanceolate, long tapering; floret 7.5-25 mm long, 1.0-1.5 mm in diameter, narrowly cylindrical; callus 2.5-5.0 mm, sharp; lemmas indurate, margins not overlapping, the upper portion fused and lacking apical lobes; awn 65-180 mm long, persistent and twice geniculate, the proximal sections twisted, the distal section straight, or flexuous to somewhat curled; palea subequal to the lemma, prow tipped, its veins extending to the apical margin. Name from Greek, hesperos, west, and Stipa.

Hesperostipa is endemic to North America. Superficially, its members appear close to the Eurasian Stipa sensu stricto because both have conspicuous morphological features that are adaptive to seasonally dry grassland habitats,

e.g., large, elongate fruits, sharp calluses, indurate lemmas, and long, persistent awns, features that help bury the seeds to a depth where soil moisture is adequate for successful establishment (Misra 1961). The palea structure, epiblast morphology, and lemma epidermal pattern all indicate that the closest extant relatives of Hesperostipa are the primarily South American genera Piptochaetium and Nassella (Barkworth & Everett 1987; Barkworth 1990).

- Hesperostipa comata (Trinius & Ruprecht) Barkworth, comb. nov. BA-SIONYM: Stipa comata Trinius & Ruprecht, Mém. Acad. Imp. Sci. Saint-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 5(1):75 (1842). HOLOTYPE: LE!; CANADA. Carlton House Fort, Saskatchewan River; Drummond.
- Hesperostipa comata (Trinius & Ruprecht) Barkworth subsp. intermedia (Scribner & Tweedy) Barkworth, comb. et stat. nov. BASIONYM: Stipa comata Trinius & Ruprecht var. intermedia Scribner & Tweedy, Bot. Gaz. 11:171 (1886). HOLOTYPE: US!; UNITED STATES. Wyoming: Yellowstone Park, Junction Butte, 6000 ft; Tweedy 610.
- Hesperostipa curtiseta (Hitchcock) Barkworth, comb. nov. BASIONYM: Stipa spartea Trinius var. curtiseta A.S. Hitchcock, Contr. U.S. Natl. Herb. 24(7):230 (1925). HOLOTYPE: US!; UNITED STATES. Montana: Hound Creek Valley; Scribner 339.
- Hesperostipa neomexicana (Thurber) Barkworth, comb. nov. BASIO-NYM: Stipa pennata L. var. neomexicana Thurber in J.M. Coulter, Man. Bot. Rocky Mt. 408 (1885). TYPE: UNITED STATES. New Mexico: Rio Mimbres; Thurber 269. Stipa neomexicana (Thurber) Scribner, Amer. Grasses II, 132, f. 428 (1899).

Weber (1957) reported a single plant that seemed, from what he described as circumstantial evidence, to be a hybrid between Achnatherum hymenoides and Hesperostipa neomezicana. It was completely sterile.

Hesperostipa spartea (Trinius) Barkworth, comb. nov. BASIONYM: Stipa spartea Trinius, Mém. Acad. Imp. Sci. Saint-Pétersbourg, Sér. 6, Sci. Math. 1:82 (1830). HOLOTYPE: LE!; North America: Rocky Mountains; "Hook. Cat. 253".

NASSELLA Desvaux

Plants cespitose. Culms unbranched (ours) or branched. Margins of basal leaves often ciliate at the throat. Glumes 5-22 mm long, tapering from near the base to the narrowly acute tip, often anthocyanic; floret terete or laterally compressed, 1-many times longer than wide; lemma indurate, papillose or tuberculate, at least above, variously pubescent, the margins strongly overlapping; lemma apex fused, forming a more or less evident neck, this often pale in color, restricted at the base, and crowned with bulbous based hairs; awn varying from short to long, short awns being associated with short, more rounded florets and long awns with cylindrical florets; palea 1/3 or less the length of the lemma, glabrous, ecostate, rounded at the tip; anthers 1, 2, or 3, ciliate, often dimorphic within a floret. LECTOTYPE: Nassella pungens Desvaux (Parodi 1947; Barkworth 1990). Name diminutive of Latin, nassa, a wicker basket with a narrow neck, a reference to the florets of some South American species.

The need to expand the traditional interpretation of Nassella has been discussed elsewhere (Barkworth 1990) and the necessary combinations made.

Nassella cernua (Stebbins & Love) Barkworth.

Nassella formicarum (Delile) Barkworth. This species is established at several sites in California and was probably introduced in the last century or early this century.

Nassella lepida (Hitchcock) Barkworth, including Stipa lepida Hitchcock var. andersonii (Vasey) Hitchcock. The variety supposedly differs in having more slender culms and a narrow, reduced panicle but the variation appears to be continuous. Crampton (1988, in litt.) observed that plants in old, unburned stands of chaparral are often reduced but plants reestablished or regenerating after burns or soil disturbance are far more robust and have rather ample panicles.

Nassella leucotricha (Trinius & Ruprecht) Pohl.

Nassella neesiana (Trinius & Ruprecht) Barkworth. This species has been found in the past on ballast dumps in the U.S.A. but there have been no recent collections.

Nassella pulchra (Hitchcock) Barkworth.

Nassella tenuissima (Hitchcock) Barkworth.

Nassella viridula (Trinius) Barkworth.

ORYZOPSIS Michaux

Inflorescence an open or closed panicle. Glumes acute, mucronate, or rounded; florets terete or laterally compressed; calluses blunt; lemmas coriaceous to indurate, their margins at least partially overlapping at maturity; awn 1-15 mm long, caducous or persistent, almost straight to once or twice geniculate and twisted below. TYPE: Oryzopsis asperifolia Michaux. Name from Latin oryza, rice, and Greek -opsis, like.

Oryzopsis, as treated here, is polyphyletic. Its type species, O. asperifolia, is quite different from the other three species (Kam & Maze 1974). Several features suggest that it is only distantly related to other Stipeae, including the other three species of Oryzopsis. These features include its twisted basaleaf blades, rudimentary cauline leaf blades, unusual callus pubescence, lemma epidermal pattern, leaf blade cross section, and floret development (Kam & Maze 1974). The problem is determining how to treat the other North American species traditionally included in Oryzopsis. Many belong in Achnatherum, q.v. Two belong in Piptatherum. This leaves three problem species, O. exigua Thurber, O. canadensis (Poiret) Torrey, and O. pungens (Torrey) Hitchcock. Morphologically, O. canadensis and O. pungens are quite similar, differing chiefly in the length and persistence of their awns, but O. exigua is quite distinct. The lemma epidermal patterns of the three are similar but, because I am not convinced they form a natural group, I have left them in Oryzopsis for the sake of nomenclatural stability.

Oryzopsis asperifolia Michaux.

Oryzopsis canadensis (Poiret) Torrey.

Oryzopsis exigua Thurber.

Oryzopsis pungens (Torrey) Hitchcock.

PIPTATHERUM P. Beauvois

Plants perennial, with intra- or extravaginal branching. Ligules 0.2-15 mm long; blades flat, involute, or folded. Panicle open or contracted, the secondary branches frequently appressed to the primary branches. Glumes subequal, obtuse to acute or acuminate; florets dorsally compressed; callus 0.1-0.5 mm, blunt, the disarticulation scar round or horizontal; lemma dark brown or black, coriaceous to indurate, from dull to shiny, only covering the margins of the palea at maturity; awn straight to somewhat twisted, readily deciduous; palea similar to the lemma in length and texture. TYPE: Piptatherum coerulescens (Desfontaines) P. Beauvois. Name from Greek pipto, fall, and ather, awn.

Freitag (1975) restricted Piptatherum to Eurasian species that were otherwise placed in Oryzopsis, but the only North American species he examined was O. asperifolia. Morphologically, Piptatherum racemosum (Smith) Barkworth and P. micranthum are so similar to the Eurasian species that it is hard to understand their exclusion. Johnson (1945a) found the North American species of Oryzopsis had a different base number from the Eurasian species (11 rather than 12) and slightly shorter chromosomes. This does not seem adequate reason to exclude them from Piptatherum given morphological similarity to other members of the genus. The lemma epidermal pattern and leaf anatomy of these two species also argues for their association with the Eurasian species (Barkworth & Everett 1987; Barkworth, unpub. data). The third species listed, P. miliaceum (L.) Cosson, is a Eurasian introduction.

Piptatherum micranthum (Trinius & Ruprecht) Barkworth, comb. nov. BASIONYM: Urachne micrantha Trinius & Ruprecht, Mém. Acad. Imp. Sci. Saint-Pétersbourg, Sér. 6., Sci. Math., Seconde Pt. Sci. Nat. 5(1):16 (1842). TYPE: North America [from Saskatchewan]. Oryzopsis micrantha (Trinius & Ruprecht) Thurber, Proc. Acad. Nat. Sci. Philadelphia 1863:78 (1863).

Piptatherum miliaceum (L.) Cosson

Piptatherum racemosum (Smith) Barkworth, comb. nov. BASIONYM:
Milium racemosum Smith in Rees, Cycl. 23:Milium No. 15 (1813).
TYPE: UNITED STATES. Pennsylvania: Lancaster; Muhlenberg. Oryzopsis racemosa (Smith) Ricker in Hitchcock, Rhodora 8:210 (1906).

PIPTOCHAETIUM Presl, nom. cons.

Blades with translucent lines between the veins. Glumes equal, longer than the floret, lanceolate, 3, 5, or 7 veined, becoming acuminate; floret usually round in cross section, from globose to cylindrical; callus usually sharp; lemma indurate, striate, often papillose above; lemma margins involute, fitting into the longitudinal groove of the palea; lemma apex fused; awn usually twice geniculate, varying from readily caducous to persistent; palea slightly longer than the lemma but similar in texture, longitudinally grooved, its apex prow tipped.

Parodi (1944) presented an excellent revision of *Piptochaetium*, which was ignored by North American taxonomists until Thomasson (1976, 1978, 1979) provided additional evidence supporting Parodi's treatment of the genus.

Piptochaetium avenaceum (L.) Parodi

Piptochaetium fimbriatum (Kunth) Hitchcock

Piptochaetium pringlei (Scribner) Parodi

Piptochaetium setosum (Trinius) Arechavaleta. This species has become established in Marin County, California. Like Piptochaetium stipoides (Trinius & Ruprecht) Hackel, it has a distinct neck, but unlike that species, the neck is more or less straight whereas the neck in P. stipoides looks like a stiff collar that has been rolled over to expose a densely papillate adaxial surface.

PTILAGROSTIS Grisebach

Plants densely cespitose; basal branching intravaginal. Blades filiform. Panicle open or closed. Glumes hyaline, ecostate or with 1 weak vein; callus blunt; lemma coriaceous, pubescent, lobed but not fused at the apex; awn often plumose below (but not in Ptilagrostis kingii [Bolander] Barkworth); palea similar in length and texture to the lemma, 2 veined, the veins terminating before the rounded, flat apex. TYPE: Ptilagrostis mongholica (Trinius) Grisebach. Name from Greek ptilo-, down (as in feather), and Agrostis, a forage grass.

Ptilagrostis was first recognized as occurring in North America by Weber (1966, 1976). Barkworth (1983) transferred the high altitude Californian endemic, P. kingii, to the genus, thereby expanding its North American representation to two taxa.

Ptilagrostis mongholica (Trinius) Grisebach subsp. porteri (Rydberg) Barkworth

Ptilagrostis kingii (Bolander) Barkworth

STIPA L.

As I interpret the genus, Stipa is not part of North America's native flora. A.S. Hitchcock (1951) lists four species as being occasionally cultivated in the U.S.A. One of these, S. splendens Trinius, is listed above as Achnatherum splendens. Stipa pennata L. is the type of Stipa and, hence, necessarily included in Stipa. Stipa tenacissima L. also belongs in that genus according to my interpretation, but I do not know the most appropriate treatment for the

Australian S. elegantissima Labillardière. It does not belong in Stipa sensu stricto but, until a definitive study is completed, nomenclatural stability is best served by keeping it there.

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